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Migration and speciation of the *Loxoconcha japonica* species group (Ostracoda) in East Asia

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Abstract. **Eighty-five fossil and Recent species of the genus *Loxoconcha* (Crustacea: Ostracoda) from East Asia are systematically reexamined. On the basis of carapace morphology, the genus *Loxoconcha* from East Asia is divided into five species groups: *L. pulchra*, *L. optima*, *L. japonica*, *L. uranouchiensis* and *L. japonica* species groups. The migration and speciation patterns of four species of the *L. japonica* species group are as follows. In Late Miocene, *L. lilljeborgii* and *L. tumulosa* were distributed over the Paleo-Indian Ocean. In Early Pliocene time, these species migrated to the Western Pacific and *L. japonica* evolved from populations of *L. tumulosa* by peramorphic evolution. In the Middle Pleistocene, *L. shanhaiensis* evolved from populations of *L. japonica* in the Ryukyu Islands by paedomorphic evolution.**

Key words: East Asia, *Loxoconcha*, Ostracoda, paedomorphic evolution, paleobiogeography, peramorphic evolution,

Introduction

The genus *Loxoconcha* was proposed by Sars (1866) with the type species *Cythere rhomboidea* Fischer (1855), based on a Recent specimen from Lervig (= Larvik), South Norway. Since then, about 550 species belonging to this genus have been identified from around the world (Kempf, 1986). The oldest fossil record is from the Eutaw Formation (late Cretaceous) of northwest Selma, Dallas City, Alabama, North America (Crane, 1965). This genus is reported from the Paleogene of four continents: North America (Hazel *et al.*, 1980; Howe, 1963; Carreño and Cronin, 1993), Australia (Mckenzie *et al.*, 1991, 1993), Africa (Cronin and Khalifa, 1979; Ahmad *et al.*, 1991) and Europe (Keij, 1957); thus its distribution had already become worldwide. Today, it is widely distributed in littoral, sublittoral and brackish-water environments throughout the world except for the polar regions (Athersuch and Horne, 1984).

The genus *Loxoconcha* is an evolutionarily successful group, with one of the highest species diversity of all ostracod genera. Its species have adapted to various habitats, often developing morphological characters in adapting to microhabitats.

In East Asia, 85 species of *Loxoconcha* have been described since 1868 when Brady reported two Recent species from Batavia, Java, present-day Indonesia (Brady, 1868). Based on carapace outlines, surface ornamentation patterns, hinge structures and muscle scar patterns, *Loxoconcha* can be classified into five species groups (Figure 1). Morphological similarity among *Loxoconcha* species is affected either by the genotype or environmental interactions or both. It is possible to estimate the relative importance of each by investigating intraspecific morphological variants and their geographical, stratigraphical and ontogenetical variability. In this study, we focus on the neritic *L. japonica* species group. We compare morphological characters among species and evaluate the presumed phylogenetic relationships among species based on inter-specific morphological similarities. Finally, we consider geographic dispersal processes and mechanisms of adaptation to local environments.

Material

This study is based mainly on Recent and fossil faunal-slides housed at Shizuoka University. Collections of *Loxoconcha* come from 35 localities (23 Recent; 12 fossil) which range geographically from Suttsu Bay (Hokkaido, Japan) to Taiwan (Figure 2 and Table 1). All figured specimens have been deposited at the Shizuoka University Museum, Japan (SUM-CO-Number).

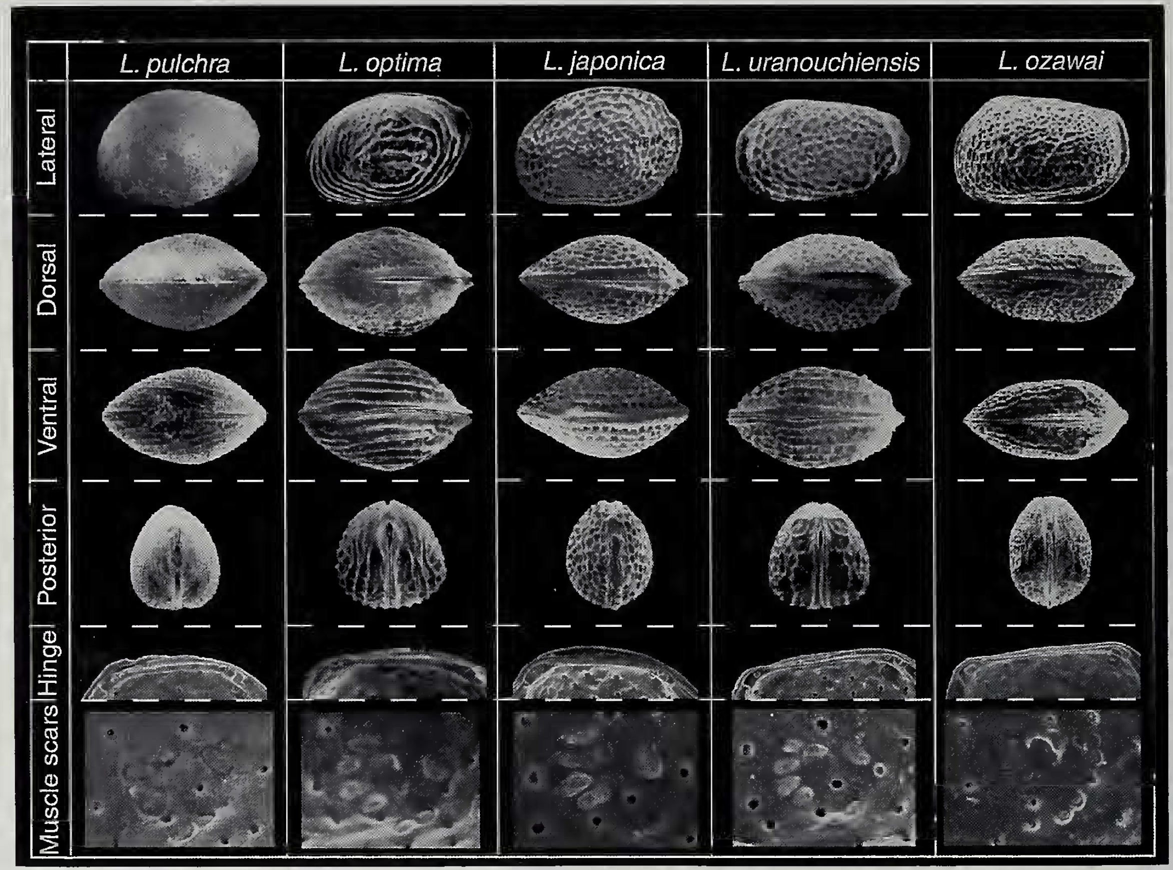


Figure 1. Five species groups of *Loxoconcha* in the East Asia, defined on the basis of their carapace morphology. Not to scale.

Morphological classifications of genus *Loxoconcha* from East Asia

Loxoconcha, which includes 85 species from the East Asia, is divided into the following five species groups on the basis of carapace morphology (Figure 1). They include those species which have not been given species names (indicated by *L.* sp.) and those referred to in quotes in the literature.

Loxoconcha pulchra *species group.* — Carapace subrhomboidal in lateral view. Surface ornamentation of the carapace consists of concentrically-arranged pits or weak reticulation, except for the dorsal area. In dorsal view, ornamentation not developed. In ventral view, five pairs of ridges diverge toward anterior. Posterior element of hingement is ball-shaped. Prominent fulcral point. A total of six species are included: *L. pulchra, L. subcirculata, L. subpulchra, L.* sp. (Hou *et al.*, 1982), *L.* sp. C (Ikeya *et al.*, 1985), "*L. pulchra*" (in Gou *et al.*, 1981).

Loxoconcha optima *species group.*—Carapace subrhomboidal in lateral view. Surface ornament of the carapace consists of concentrically-arranged ridges or pits as located around the position of the muscle scar, except for the dorsal area. In dorsal view, ornamentation not developed. In ventral view, five pairs of ridges run parallel from anterior to posterior. Posterior element of hingement is composed of three teeth. Prominent fulcral point. A total of sixteen species are included: *L. chinzeii, L. hemicrenulata, L. ikeyai, L. medioconvexa, L. optima, L. orientarica, L. pleistocenica, L. taiwanensis, L. tamakazura, L. tarda, L.* sp. (Hu, 1978), *L.* sp. (Ishizaki, 1984), *L.* sp. (Yajima, 1988), "*L. pulchra*" (in Yajima, 1988), "*L. sinensis*" (in Gou *et al.*, 1981), "*L. sinensis*" (in Zhao *et al.*, 1985).

Loxoconcha japonica *species group.*—Carapace subrhomboidal in lateral view. Surface ornament of the carapace consists of concentrically- arranged pits or coarse reticulation centered around the muscle scars. In dorsal view, a pair of ridges converges toward the anterior. In ventral view, five pairs of ridges developed that run parallel from anterior to posterior. Posterior element of hingement is ball-shaped. Fulcral point not prominent. The following four species are included: *L. japonica, L. lilljeborgii, L. shanhaiensis, L. tumulosa.*

Loxoconcha uranouchiensis *species group.*—Carapace

Table 1. Sample localities for *L. japonica* species group from East Asia. Sample numbers corresponds to those in Figure 2. Abbreviations: Alg. = Algae; M. = Mud; St. = Silt; Sd = Sand; R. = Rock; f. = fine; m. = medium; c. = coarse; mdy. = muddy; sdy. = sandy; gry. = gravelly; L. = late; M. = middle; E. = early; Ls. = Limestone; Pref. = Prefecture; Penin. = Peninsula; Is. = Island; Ja = *L. japonica* ; Sh = *L. shanhaiensis* ; Tu = *L. tumulosa* ; Li = *L. lilljeborgii.*

Recent materials

Sample number	Localities	Latitude (N)	Longitude (E)	Depth (m)	Remarks	Species
1a	Suttu Bay	42°48.9′	140°18.0′	22	R.	Ja
1b	〃	42°47.8′	140°16.2′	34	f.-Sd.	Ja
1c	〃	42°47.2′	140°18.7′	9	R.	Ja
1d	〃	42°47.2′	140°15.6′	26	f.-Sd.	Ja
1e	〃	42°46.7′	140°17.9′	11	f.-Sd.	Ja
1f	〃	42°46.7′	140°15.6′	17	f.-Sd.	Ja
1g	〃	42°46.2′	140°16.5′	7	c.-Sd.	Ja
1h	〃	42°46.2′	140°15.0′	5	c.-Sd.	Ja
2	Otsuchi Bay	39°19.6′	141°55.0′	15	c.-Sd.	Ja
3	Imagawa	38°24.6′	139°28.1′	0	Alg.	Ja
4	Aikawa	38°02.4′	138°14.3′	0	Alg.	Ja
5	Hayase	35°37.0′	135°54.7′	1	Alg.	Ja
6	Kagoshima	35°39.5′	134°46.8′	0	Alg.	Ja
7	Off Shimane	36°13.9′	133°06.0′	96	mdy., f.-m.-Sd.	Ja
8	Misaki	35°09.5′	139°37.0′	0	Sea glass	Ja
9	Osezaki	35°06.3′	138°47.4′	1	Alg.	Ja
10	Ago Bay	34°57.1′	136°40.5′	7	f.-Sd.	Ja
11	Hanesaki	33°22.0′	134°02.4′	0	Alg.	Ja
12	Uwajima Bay	33°10.8′	132°29.9′	5	v. c.-Sd.	Ja
13	Tsuyasaki	33°47.4′	130°27.7′	2	m.-Sd.	Ja
14	Danjyo Islands	32°01.9′	128°23.1′	86	f.-Sd.	Ja
15	Okawa-minato	31°14.6′	130°24.8′	0	Alg.	Ja
16	Tanega-shima Is.	30°10.3′	130°52.7′	96	c. shelly-Sd.	Ja
17	Amami-o-shima Is.	28°07.5′	129°22.0′	4	coral Sd.	Ja, Sh
18	Tokuno-shima Is.	27°51.6′	128°57.7′	0	Alg.	Ja, Tu
19	Yoron Is.	27°02.9′	128°27.3′	0	Alg.	Ja, Sh, Tu, Li
20a	Nago Bay	26°34.1′	127°56.4′	38	m.-St.	Sh
20b	〃	26°39.3′	127°51.5′	59	m.-Sd.	Ja, Sh
20c	〃	26°37.7′	127°52.2′	22	m.-Sd.	Ja, Sh
20d	〃	26°36.1′	127°53.5′	40	c.-Sd	Ja, Sh
20e	Nakagusuku Bay	27°19.2′	127°52.0′	4	sdy.-M.	Ja, Li
20f	〃	26°16.8′	127°50.3′	6	gry.-Sd.	Sh, Li
20g	〃	26°15.9′	127°54.3′	21	Sd.	Ja, Sh, Tu, Li
20h	〃	26°15.3′	127°53.1′	4	gry.-Sd.	Ja, Sh
20i	〃	26°15.0′	127°52.3′	20	Sd.	Ja, Sh
20j	〃	26°12.8′	127°55.0′	48	Sd.,-M.	Ja, Sh, Li
20k	〃	26°12.5′	127°52.9′	28	mdy.-Sd.	Ja, Sh, Li
20l	〃	26°10.1′	127°52.8′	22	Sd.	Ja, Sh
20m	〃	26°07.8′	127°53.9′	70	gry.-Sd.	Ja, Sh, Li
21	Off Miyako Is.	24°47.9′	127°37.4′	124	c.-Sd.	Sh
22	Sekisei-sho	24°27.4′	124°03.3′	167	f.-Sd.	Ja, Sh
23	Hengchun Penin.	21°56.0′	120°49.0′	0	Alg.	Sh, Tu

Fossil materials

Sample number	Formation (age)	Localities	Latitude (N)	Longitude (E)	Remarks	Species
a	Hamada (L. Pleistocene)	Shimokita Penin.	41°10.3′	141°16.4′		Ja
b1	Sawane (Pliocene)	Sado Is.	37°59.6′	138°15.6′		Ja
b2	Sawane (Pliocene)	〃	37°59.3′	138°15.9′		Ja
c1	Hiradoko (L. Pleistocene)	Noto Penin.	37°27.0′	137°18.2′		Ja
c2	Miyainu (L. Pleistocene)	〃	37°20.2′	137°13.8′		Ja
c3	Numashiro (L. Pleistocene)	〃	35°19.4′	139°15.4′		Ja
d1	Ninomiya (L. Pleistocene)	Oiso Hill	35°18.9′	139°15.1′		Ja
d2	〃	〃	35°18.4′	139°15.4′		Ja
d3	〃	〃	35°18.2′	139°15.7′		Ja
e	Takahama (Holocene)	Fukui Pref.	35°29.2′	135°33.3′		Ja
f	Hamamatsu (Holocene)	Hamana-ko	34°44.8′	137°36.5′		Ja
g	Ananai (Plio-Pleistocene)	Shikoku	33°29.4′	133°56.7′		Ja
h	Shimo-jiro (M. Pleistocene)	Okino-erabu Is.	27°24.5′	128°38.3′		Sh
i	Maja (E. Pliocene)	Kume Is.	26°22.6′	126°47.4′		Ja
j1	Yonabaru (L. Pliocene)	Okinawa Is.	26°09.7′	127°46.7′		Ja
j2	Chinen Sand (E. Pleistocene)	Okinawa Is.	26°07.3′	127°43.8′		Ja
k	Tungshiao (L. Pleistocene)	Taiwan	24°36.0′	120°43.0′		Sh
l1	Hengchun Ls. (L. Pleistocene)	Taiwan	21°59.0′	120°43.0′		Ja, Sh, Li
l2	Hengchun Ls. (L. Pleistocene)	Taiwan	21°55.0′	120°51.0′		Sh, Tu

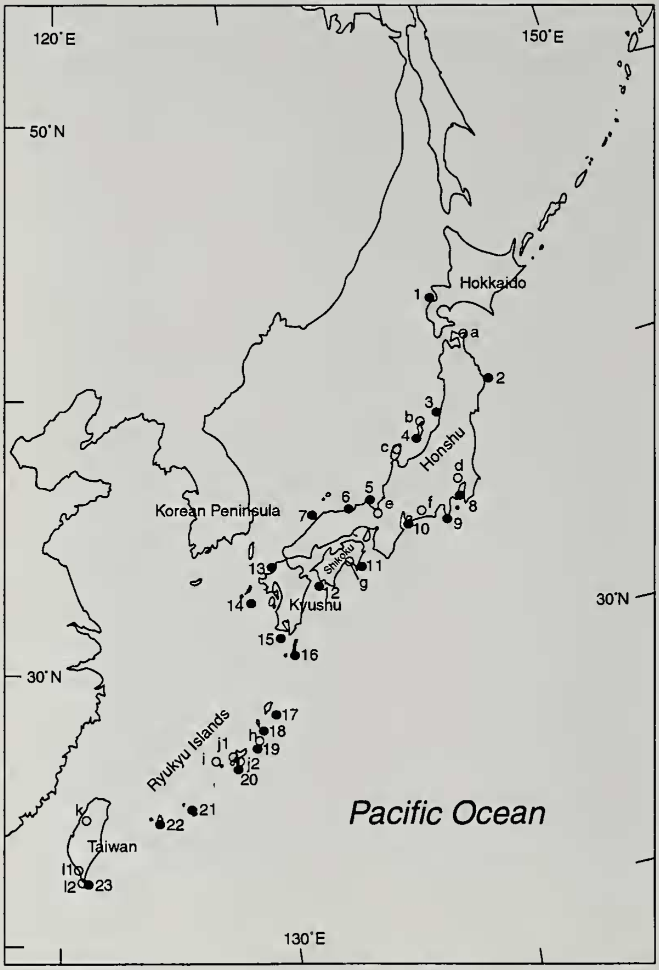


Figure 2. Map showing sampling localities. Numbers and lower case letters correspond to the sample numbers in Table 1.

subrhomboidal to oblong in lateral view. Surface ornament of the carapace consists of reticulation. In dorsal view, the carapace is covered with irregular reticulation. In ventral view, three- or four-pairs of ridges run parallel from anterior to posterior, the most ventral pair being developed only in the anterior region. Posterior element of hingement is ball-shaped. Prominent fulcral point. A total of forty-three species are included: *L. bispinosa, L. bizenensis, L. brevia, L. crassela, L. crispatum, L. epeterseni, L. hanachirusato, L. harimensis, L. hattorii, L. kattoi, L. kitanipponica, L. malayensis, L. nozokiensis, L. paiki, L. pashihaiensis, L. prolaeta, L. sinensis, L. tata, L. tosaensis, L. tosamodesta, L. triconicula, L. uranouchiensis, L. ventispina, L. viva, L. xuwenensis, L. yinggehaiensis, L. zamia, L. zhejiangensis, L.* sp. A (Huh, 1992), *L.* sp. B (Ishizaki, 1968), *L.* sp. B (Lee, 1990), *L.* sp. C (Huh, 1992), *L.* sp. 2 (Yamane, 1998), "*L. hattorii*" (in Cai, 1982), "*L. hattorii*" (in Wang and Zhang, 1987), "*L. kattoi*" (in Ruan and Hao, 1988), "*L. sinensis*" (in Gou *et al.*, 1981), "*L. sinensis*" (in Ruan and Hao, 1988), "*L. uranouchiensis*" (in Cai and Chen, 1987), "*L.* cf. *uranouchiensis*" (in Gou *et al.*, 1983), "*L. uranouchiensis*" (in Tabuki *et al.*, 1987), "*L. uranouchiensis*" (in Yamane, 1998), "*L. viva*" (in Wang *et al.*, 1988).

Loxoconcha ozawai *species group.*—Carapace subrhomboidal to oblong in lateral view. Surface ornamentation of the carapace consists of weak reticulation. In dorsal view, the carapace is covered with weak, irregular reticulation. In ventral view, two pairs of weak ridges converge toward anterior. Posterior element of hingement is ball-shaped. Prominent fulcral point. The following sixteen species are included: *L. binhaiensis, L. elliptica, L. fujianensis, L. gigantea, L. hataii, L. ocellata, L. ozawai, L. subkotoraforma, L.* sp. (Ikeya *et al.*, 1992), *L.* sp. (Tsukagoshi and Kamiya, 1996), *L.* sp. B (Huh, 1992), *L.* sp. B (Ishizaki, 1971), *L.* sp. D (Huh, 1992), *L.* sp. 1 (Ozawa, 1996), *L.* sp. 1 (Yamane, 1998), "*L. sinensis*" (in Zhao and Wang, 1988).

Natural history of *Loxoconcha japonica* species group

Morphological characters

In order to characterize the *L. japonica* species group, four species of the group were compared in terms of carapace morphology (Figures 3, 4), pore system (Figure 5), appendages (Figure 6) and male copulatory organ (Figure 7). The following summarizes the morphology of this species group.

Carapace outline.—Carapace subrhomboidal in lateral view. Dorsal margin straight and sloped toward anterior or arched dorsally; anterior margin with an oblique curvature; ventral margin slightly concave at mid-anterior area; posterior margin curved toward the dorsal. Caudal process protrudes prominently toward posterodorsal. In dorsal and ventral view, carapace diamond- to wedge-shaped. In posterior view, carapace elliptical to egg-shaped. Large sexual dimorphism; in lateral view, male more elongate.

Carapace ornamentation.—Surface of the carapace is entirely ornamented with pits or coarse reticulation in lateral view. The ornamentation is concentrically arranged, consisting of eight rings centered around the position of the muscle scar. Posteroventral alate ridge and/or posterodorsal protuberance are/is sometimes developed. In ventral view, five pairs of ridges run parallel from the anterior to posterior margins. In dorsal view, a pair of ridges converges toward the anterior. In posterior view, on the ventral side of the posterior margin, four pairs of short ridges are developed that consist of reticulations arranged parallel to the posterior margin. On the dorsal side of the posterior margin, on the other hand, radially-developed ridges centered near the position of the caudal process intersect ridges that parallel the posterior margin.

Hinge.—Gongylodont. In left valve, anterior element is

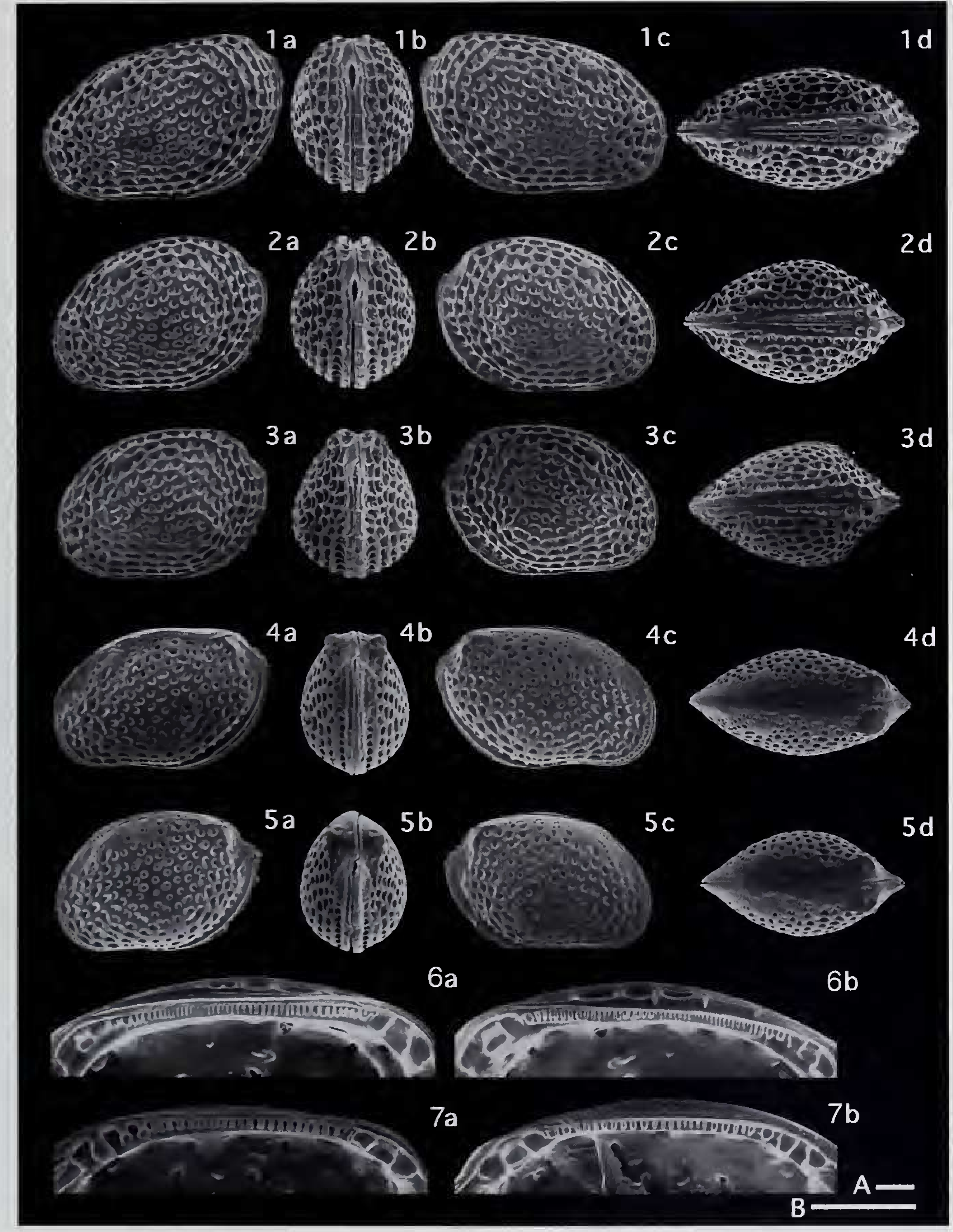


Figure 3. 1-3, 6. *Loxoconcha japonica* Ishizaki, 1968. 4, 5, 7. *Loxoconcha lilljeborgii* Brady, 1868. 1. A male carapace of the same specimen in external left lateral view (**a**), posterior view (**b**), right lateral view (**c**) and dorsal view (**d**) from sample no. 8 (SUM-CO-1269). 2. A female carapace of the same specimen in external view (**a**-**d**) from sample no. 8 (SUM-CO-1270). 3. A female carapace of the same specimen with alate ridge at the posteroventral area in external view (**a**-**d**) from sample no. 17 (SUM-CO-1271). 4. A male carapace of the same specimen in external view (**a**-**d**) from sample no. 19 (SUM-CO-1305). 5. A female carapace of the same specimen in external view (**a**-**d**) from sample no. 19 (SUM-CO-1306). 6. Hingement of female right (**a**) (SUM-CO-1272) and left (**b**) (SUM-CO-1273) valves from sample no. 19. 7. Hingement of female right (**a**) (SUM-CO-1307) and left (**b**) (SUM-CO-1308) valves from sample no. 19. Scale bars = 100 μm (A for 1-5; B for 6, 7).

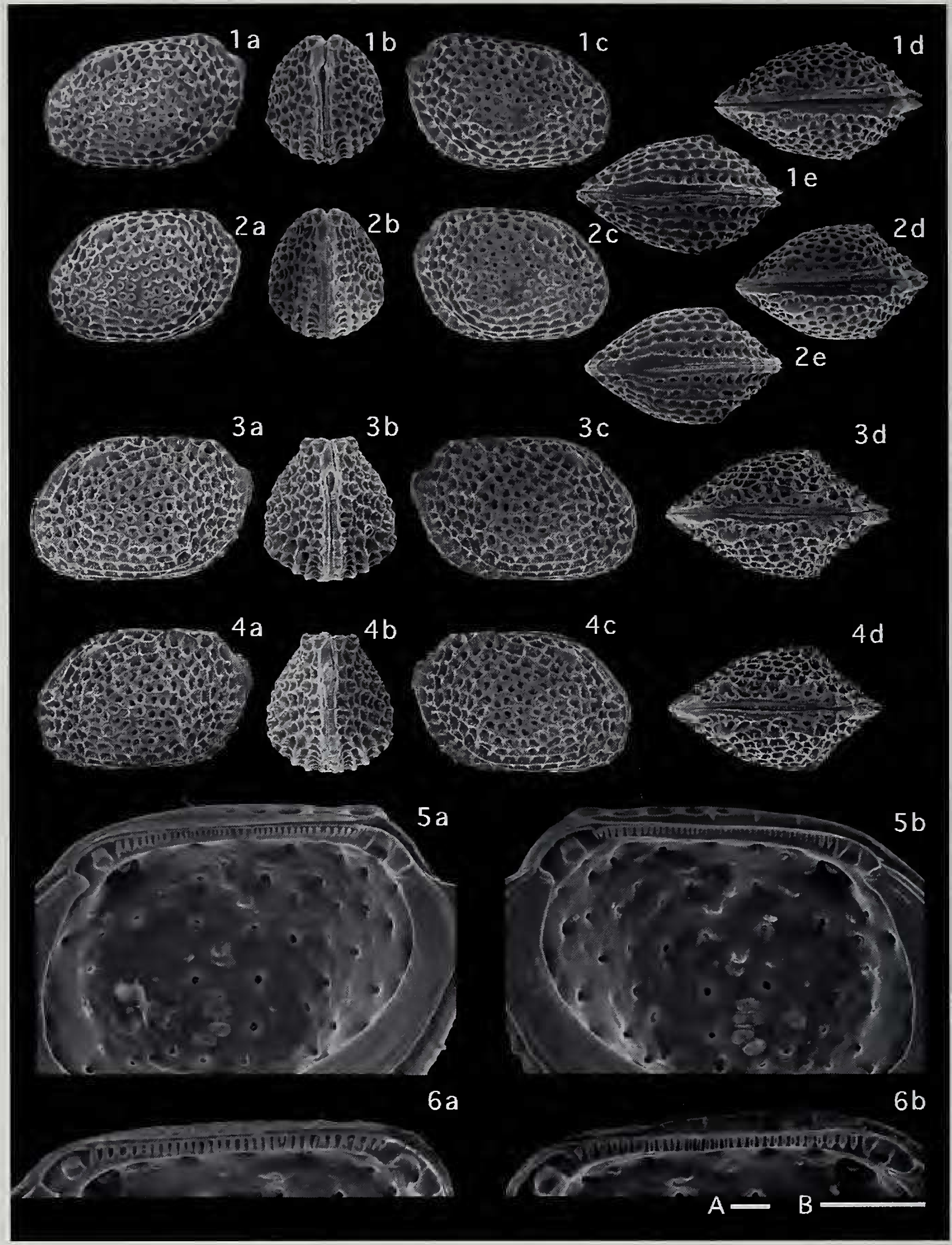


Figure 4. **1, 2, 5.** *Loxoconcha shanhaiensis* Hu, 1981. **3, 4, 6.** *Loxoconcha tumulosa* (Hu, 1979). **1.** A male carapace of the same specimen in external left lateral view (**a**), posterior view (**b**), right lateral view (**c**), dorsal view (**d**) and ventral view (**e**) from sample no. 17 (SUM-CO-1284). **2.** A female carapace of the same specimen in external view (**a–e**) from sample no. 17 (SUM-CO-1285). **3.** A male carapace of the same specimen in external view (**a–d**) from sample no. 23 (SUM-CO-1294). **4.** A female carapace of the same specimen in external view (**a–d**) from sample no. 23 (SUM-CO-1295). **5.** Hingement and muscle scars of female right (**a**) (SUM-CO-1286) and left (**b**) (SUM-CO-1287) valves from sample no. 20h. **6.** Hingement of female right (a) (SUM-CO-1296) and left (b) (SUM-CO-1297) valves from sample no. 23. Scale bars = 100 μm (A for 1-4; B for 5, 6).

a down-turned claw, median element with 25–51 teeth, and posterior element is ball-shaped.

Ocular sinus.—In all four species, nipple-like projection develops at the dorsoposterior portion in internal view.

Muscle scars.—Four adductor muscle scars in an arcuate row, concave anterior. The upper of the two middle ones is larger than the rest. A bean-shaped frontal scar of occurs in front of the lower two adductor muscle scars. Two mandibular scars in front and below the lowest adductor muscle scar. Fulcral point absent.

Pore system.—In all species, 83 sieve-type pores are distributed in each adult valve, and each pore opening location resembles among four species (left side of Figure 5). Distribution of radial pores falls into two patterns (right side of Figure 5), depending on numbers of pores extending to marginal area: a), 11 in anterior area and 5 in posterior area: *L. japonica*, *L. shanhaiensis* and *L. tumulosa*; b), 10 and 5, respectively: *L. lilljeborgii*. Moreover, *L. lilljeborgii* is differentiated from the other three species, in that

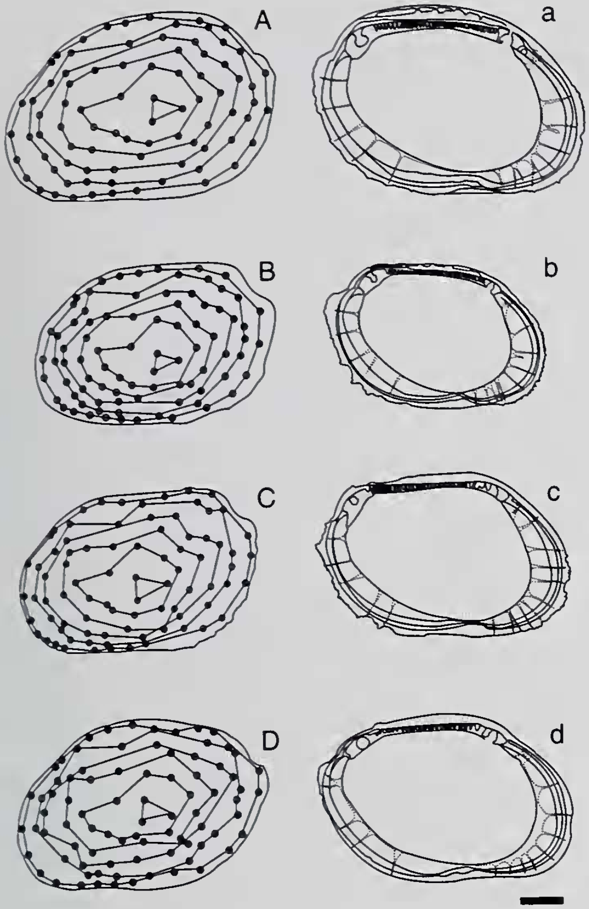


Figure 5. The pattern of distribution pores in external view (A–D) and the radiation of radial pores in internal view (a–d) on four species of the *Loxoconcha japonica* species group (all specimens are female left valves). **A, a.** *Loxoconcha japonica* Ishizaki, 1968 (A, SUM-CO-1262; a, SUM-CO-1263). **B, b.** *Loxoconcha shanhaiensis* Hu, 1981 (B, SUM-CO-1274; b, SUM-CO-1275). **C, c.** *Loxoconcha tumulosa* (Hu, 1979) (C, SUM-CO-1288; c, SUM-CO-1289). **D, d.** *Loxoconcha lilljeborgii* Brady, 1868 (D, SUM-CO-1298; d, SUM-CO-1299). Scale bar = 100 μm.

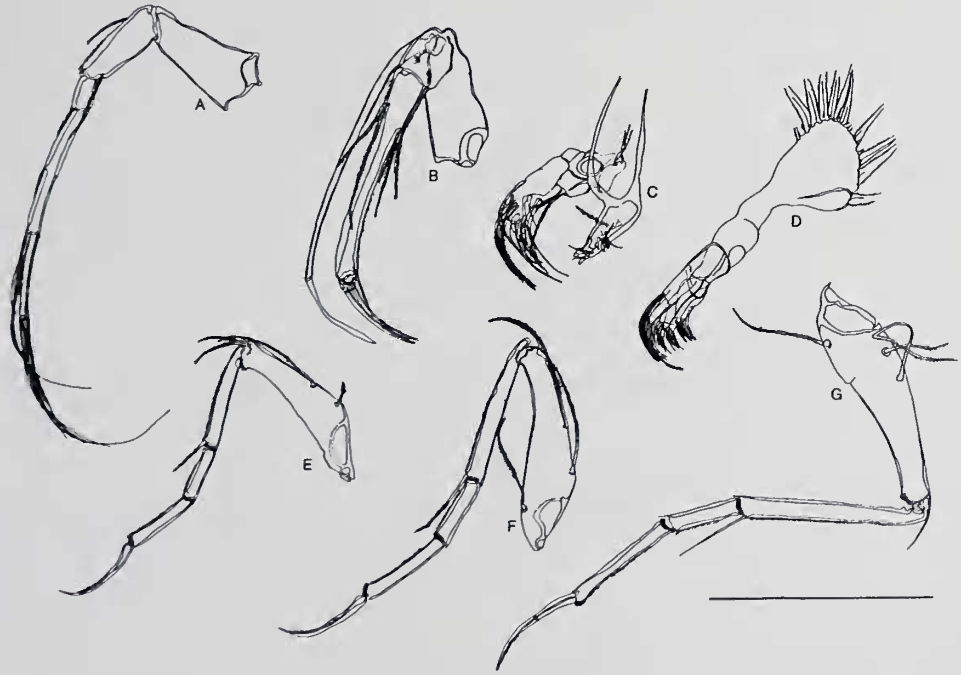


Figure 6. Chitinous parts of *Loxoconcha shanhaiensis* Hu, 1981 from sample no. 20f. **A**, antennule; **B**, antenna (SUM-CO-1277); **C**, mandible; **D**, maxilla (SUM-CO-1278); **E**, first thoracic leg; **F**, second thoracic leg; **G**, third thoracic leg (SUM-CO-1279). Scale bar = 50 μm.

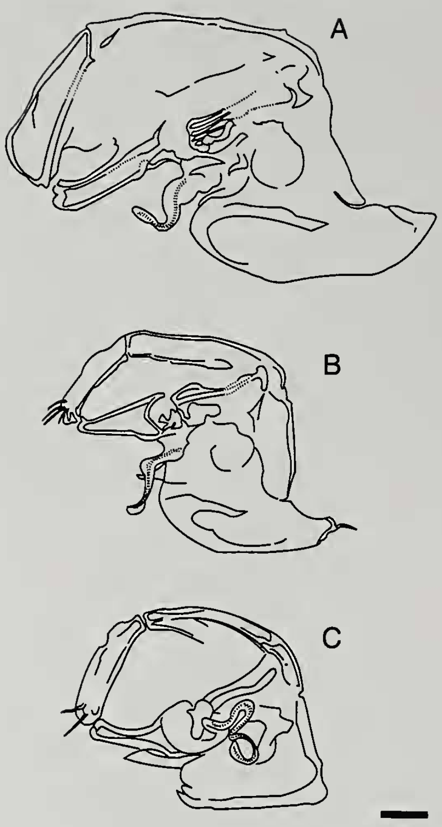


Figure 7. Male copulatory organs of three species of *Loxoconcha japonica* species group. **A.** *Loxoconcha japonica* Ishizaki, 1968 from sample no. 8 (SUM-CO-1264). **B.** *Loxoconcha shanhaiensis* Hu, 1981 from sample no. 20f (SUM-CO-1276). **C.** *Loxoconcha lilljeborgii* Brady, 1868 from sample no. 19 (SUM-CO-1300). Scale bar = 50 µm.

the upper two pores of at the posterior margin branch in the middle of the marginal infoldment.

Appendages.—No significant differences are observed among the four species.

Male copulatory organ.—Except for *L. tumulosa*, outline of the basal capsule is trapezoidal and costa are developed in three species. In detail, however, several differences are observed among the three species in morphology of the copulatory organ. Distal corner rounded in *L. lilljeborgii* but tapered in *L. japonica* and *L. shanhaiensis*; ductus ejaculatorius curved in *L. lilljeborgii* but shoehorn-shaped in *L. japonica* and *L. shanhaiensis*; clasping apparatus absent in *L. japonica*, triangular in *L. shanhaiensis* and square in *L. lilljeborgii*.

Ontogenetic differentiation in carapace morphology

For the carapace morphologies of the four species, the ontogenetic differentiation from the A–2 instar to the adult were compared.

Carapace outline (Figure 8).—The position of the maximum height shifts toward the posterior from the A–2 instar to the adult. The time of shift is at the A-1 instar for *L. japonica* and *L. lilljeborgii* and at the adult for *L. shanhaiensis* and *L. tumulosa*.

The position of the maximum width is stationary from the A–2 instar to the adult (*L. shanhaiensis* and *L. tumulosa*) or shifts to the anterior at the adult (*L. lilljeborgii* and the male of *L. japonica*).

Carapace ornamentation (Figure 8).—The concentric arrangement of reticulation or pits is fixed from the A–2 instar to the adult. From the A–2 instar to the adult, the developmental state of reticulation or pits, however, differs from species to species. Namely, *L. japonica* already has adult-like coarse reticulation in the A–2 instar, but *L. shanhaiensis* and *L. tumulosa* only attain coarse reticulation in the A-1 instar. *L. lilljeborgii* has pits in the A–2 and A–1 instars, and is smoothly reticulate in the adult.

The posteroventral alate ridge is well developed in the A–2 and A–1 instars of all four species. In the adult, this character is retained in *L. shanhaiensis* and *L. tumulosa*, but disappears in *L. lilljeborgii* and the male of *L. japonica*. In the female of *L. japonica*, however, some specimens keep and others lose this character.

The posterodorsal protuberance does not appear during ontogenetic development in *L. japonica* and *L. shanhaiensis*, whereas, it appears from the A–1 instar onward in *L. tumulosa* and *L. lilljeborgii*.

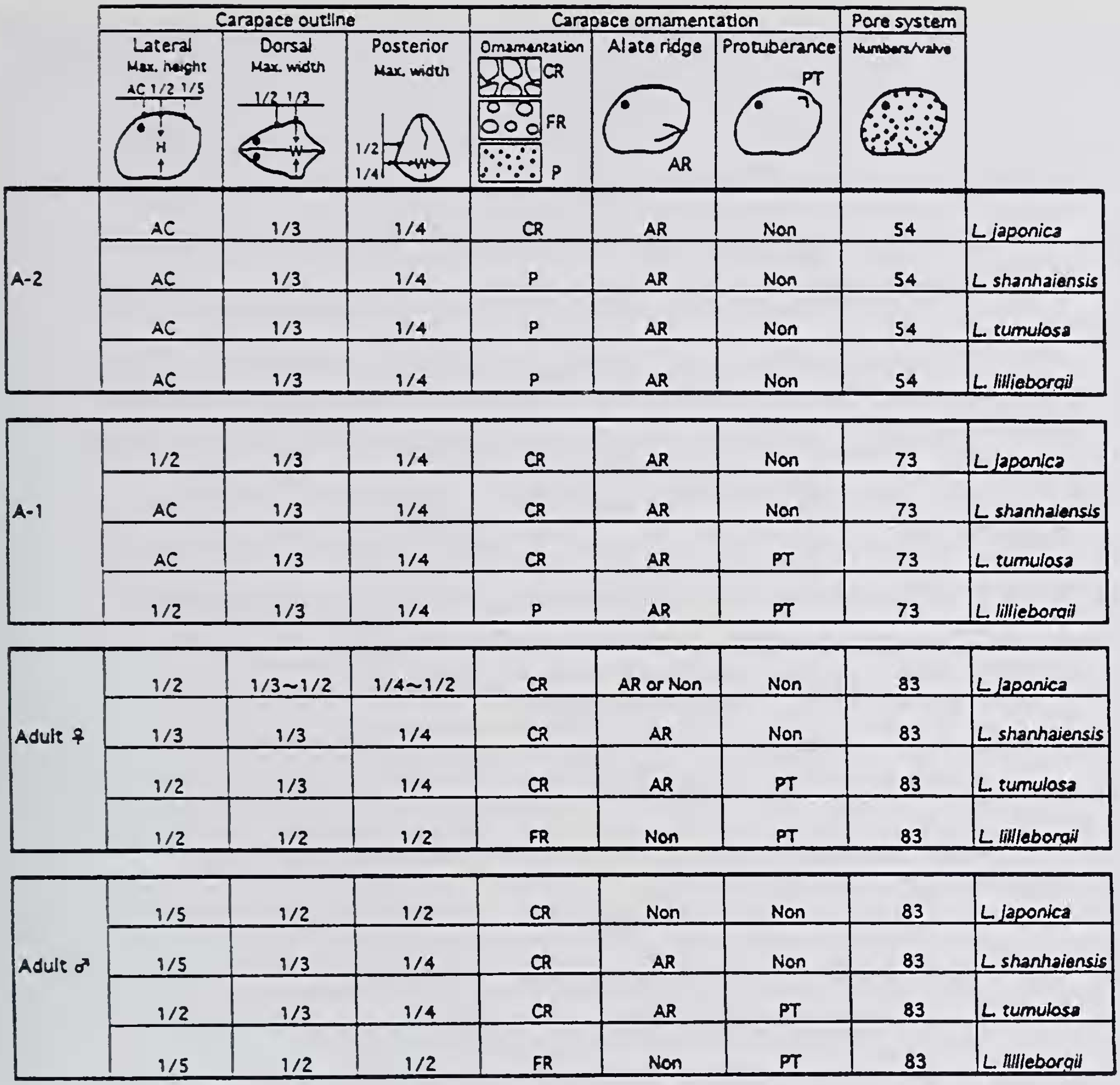
Hinge (Figure 9).—Although development of the anterior element of the hinge is weak in the A–2 instar, these species clearly possess a gongylodont hinge after the A–1 instar. The number of teeth in the median element could not be counted in the A–2 instar, since it is smooth, however, from the A–1 instar onward the number of teeth is: 42–51 in *L. japonica*, 39–40 in *L. shanhaiensis*, 31–40 in *L. tumulosa*, and 25–31 in *L. lilljeborgii*.

Ocular sinus (Figure 9).—The nipple-like projection in the dorsoposterior area on the internal side appears after the A–2 instar for *L. japonica, L. shanhaiensis* and *L. tumulosa* and after the A–1 instar for *L. lilljeborgii*.

Muscle scars (Figure 4).—After the A–2 instar, the four species have four adductor muscle scars in an arcuate row; with no morphological variation in this feature among the species.

Pore system (Figure 8).—The total number of sieve-type pores per valve is the same in all four species: 54 in the A–2 instar, 73 in the A–1 instar and 83 in the adult.

From the carapace characters described above, it is thought that *L. japonica*, *L. lilljeborgii* and an ancestor of *L. shanhaiensis-L. tumulosa* differentiated at the A–2 instar, and that *L. shanhaiensis* and *L. tumulosa* differentiated in the A–1 instar (Figure 10).


AC 1/2 1/5
H
1/2 1/3
W
1/2
1/4
W'
CR
FR
P
AR
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	Carapace outline			Carapace ornamentation			Pore system	
	Lateral Max. height	Dorsal Max. width	Posterior Max. width	Ornamentation	Alate ridge	Protuberance	Numbers/valve	
A-2	AC	1/3	1/4	CR	AR	Non	54	*L. japonica*
	AC	1/3	1/4	P	AR	Non	54	*L. shanhaiensis*
	AC	1/3	1/4	P	AR	Non	54	*L. tumulosa*
	AC	1/3	1/4	P	AR	Non	54	*L. lillieborgii*
A-1	1/2	1/3	1/4	CR	AR	Non	73	*L. japonica*
	AC	1/3	1/4	CR	AR	Non	73	*L. shanhaiensis*
	AC	1/3	1/4	CR	AR	PT	73	*L. tumulosa*
	1/2	1/3	1/4	P	AR	PT	73	*L. lillieborgii*
Adult ♀	1/2	1/3~1/2	1/4~1/2	CR	AR or Non	Non	83	*L. japonica*
	1/3	1/3	1/4	CR	AR	Non	83	*L. shanhaiensis*
	1/2	1/3	1/4	CR	AR	PT	83	*L. tumulosa*
	1/2	1/2	1/2	FR	Non	PT	83	*L. lillieborgii*
Adult ♂	1/5	1/2	1/2	CR	Non	Non	83	*L. japonica*
	1/5	1/3	1/4	CR	AR	Non	83	*L. shanhaiensis*
	1/2	1/3	1/4	CR	AR	PT	83	*L. tumulosa*
	1/5	1/2	1/2	FR	Non	PT	83	*L. lillieborgii*

Figure 8. Schematic diagram of ontogenetic differentiation of carapace morphology. Abbreviations: AC = anterior cardinal angle, H = maximum height, W = maximum width on dorsal view, W' = maximum width on posterior view, CR = coarse reticulation, FR = fine reticulation, P = pit, AR = alate ridge, PT = protuberance.

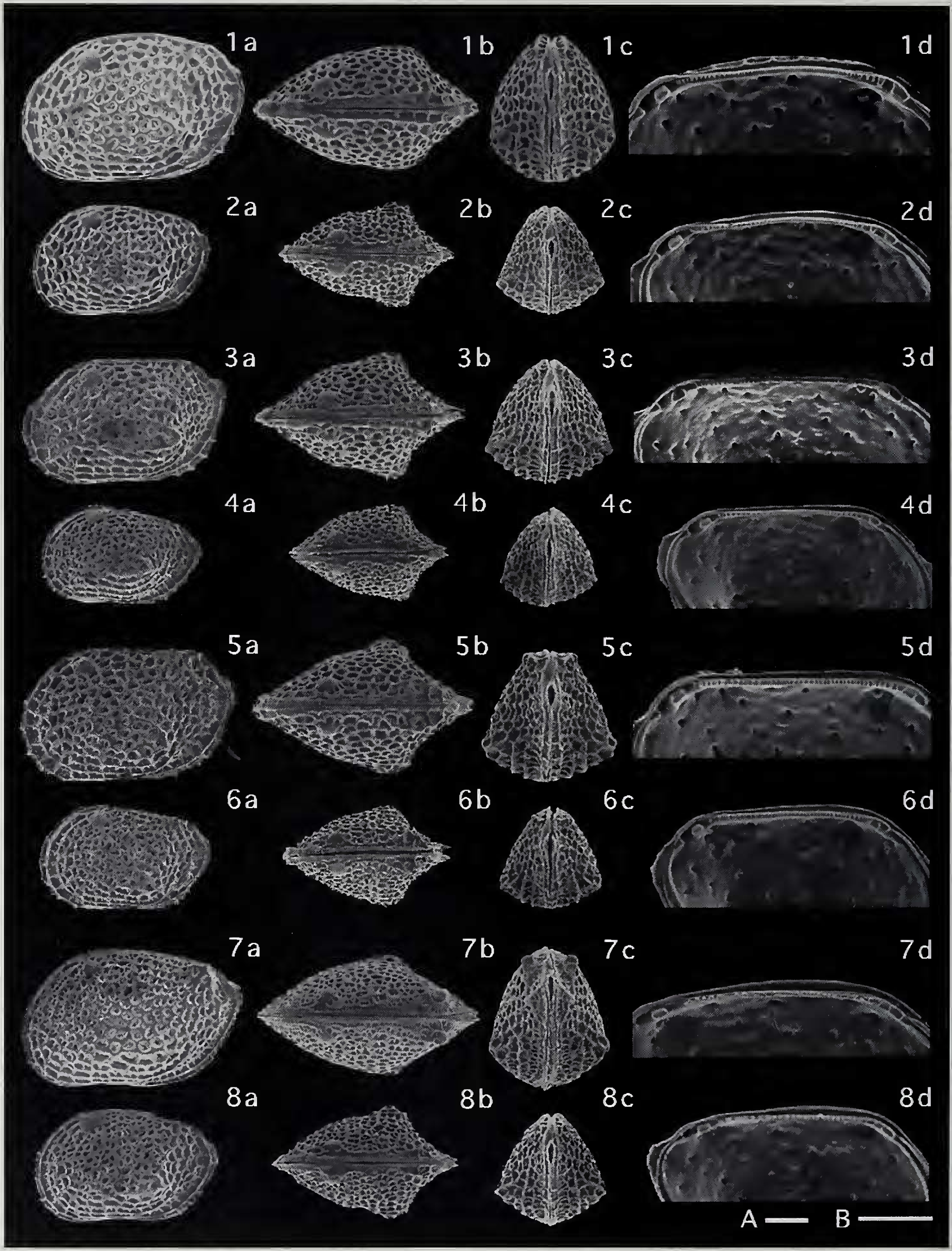
Paleobiogeography

On the basis of our materials and published reports, we considered the paleobiogeographic distributions of the four species.

Fossil distribution (Figure 11).—The oldest specimens of *L. lilljeborgii* and *L. tumulosa* occur in the Late Miocene Round Chalk and Silt Formation from the Andaman Islands of the Indian Ocean (Loc. A: Guha, 1968). Two species are also reported from the Pliocene Guiter Formation from the same region (Loc. A': Guha, 1968). These two species, however, occur also in the Late Pleistocene in the West Pacific region. Namely, *L. lilljeborgii* occurs from the Late Pleistocene Hengchun Limestone from Taiwan (Loc. E: Figure 2, 11) and in the Late Pleistocene Gundurimba Clay from Australia (Loc. C: McKenzie and Pickett, 1984), and *L. tumulosa* occurs from the Late Pleistocene Hengchun Limestone from Taiwan (Loc. D: Figure 2, loc. 12).

The oldest specimen of *L. japonica* comes from the Early Pliocene Maja Formation from Kume Island of the Ryukyus (Loc. G: Figure 2, loc. i). This species also occurs in thirteen post-Pliocene formations ranging from Taiwan to the northern part of Honshu (Locs. D, H and J–S) and in Holocene sediments from Hong Kong (Loc. B: Cao, 1998).

The oldest fossil occurrence of *L. shanhaiensis* is known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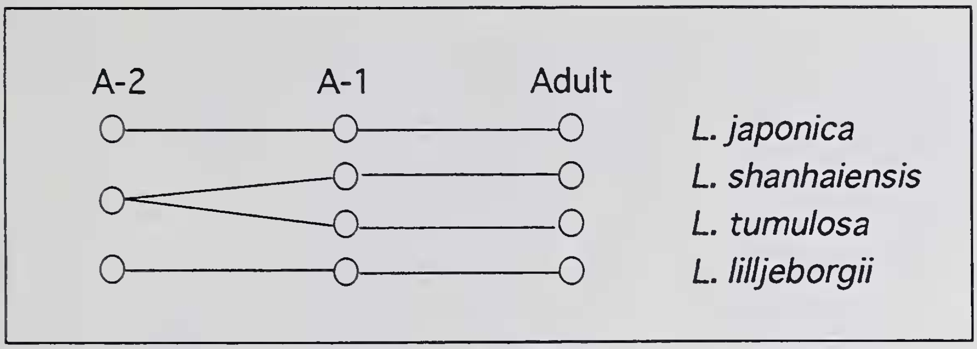

Figure 10. Ontogenetic differentiation of four species based on carapace characters.

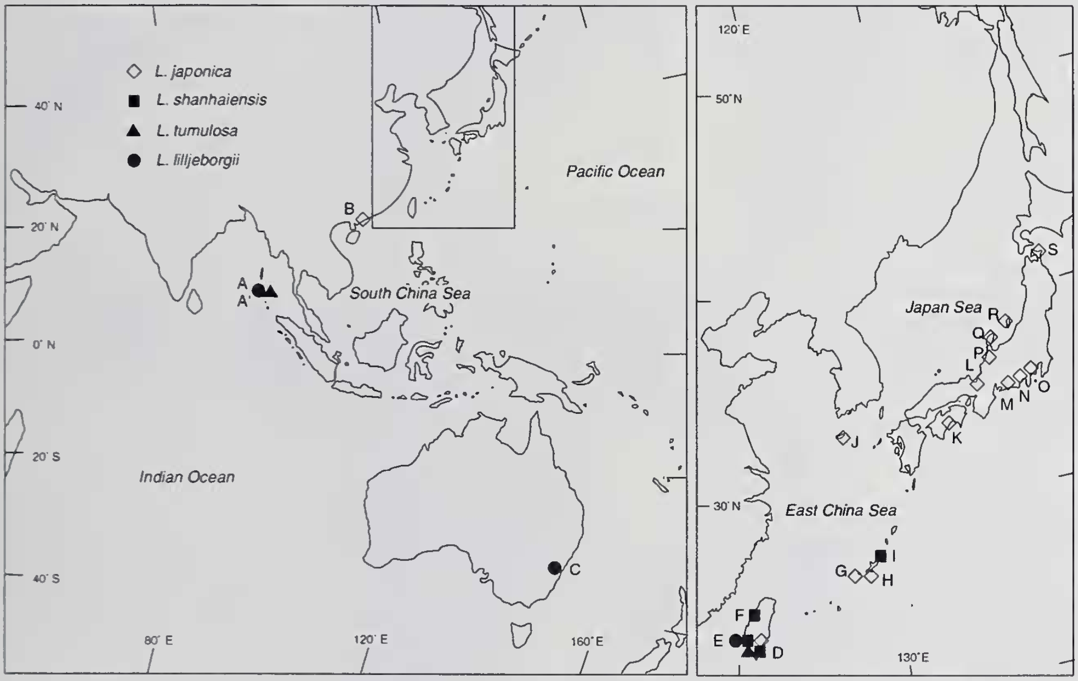

Figure 11. Geographic distribution of four species of *Loxoconcha japonica* species group (fossil). A and A' (Late Miocene Round Chalk and Silt Formation and Pliocene Guiter Formation; Guha, 1968); **B** (Holocene Hang Hau Formation; Cao, 1998); **C** (Late Pleistocene Gundurimba Clay; McKenzie and Pickett, 1984); **D** (Late Pleistocene Hengchun Limestone; Hu, 1979); **E** (Late Pleistocene Hengchun Limestone; Hu, 1981); **F** (Late Pleistocene Tungshiao Formation; Hu, 1986); **G** (Early Pliocene Maja Formation); **H** (Early Pleistocene Chinen Sand); **I** (Middle Pleistocene Shimojiro Formation); **J** (Early Pleistocene Sogwipo Formation and Middle Pleistocene Shinyangri Formation; Lee, 1990); **K** (Plio-Pleistocene Ananai Formation); **L** (Holocene Takahama shell bed); **M** (Holocene Hamamatsu Formation); **O** (Holocene bore hole core samples; Irizuki *et al.*, 1998); **P** (Plio-Pleistocene Omma Formation; Ozawa, 1996); **Q** (Late Pleistocene Miyainu and Numashiro formations); **R** (Pliocene Sawane Formation); **S** (Late Pleistocene Hamada Formation).

⬅ **Figure 9.** Juvenile specimens of *Loxoconcha japonica* species group. **1**, **2**. *Loxoconcha japonica* Ishizaki, 1968. **3**, **4**. *Loxoconcha shanhaiensis* Hu, 1981. **5**, **6**. *Loxoconcha tumulosa* (Hu, 1979). **7**, **8**. *Loxoconcha lilljeborgii* Brady, 1868. **1**. A-1 stage carapace of same specimen in external left lateral view (**a**), dorsal view (**b**) and posterior view (**c**) from sample no. 8 (SUM-CO-1265), and hingement of the same stage of left valve (**d**) from sample no. 8 (SUM-CO-1266). **2**. A-2 stage carapace of same specimen in external view (**a**-**c**) from sample no. 8 (SUM-CO-1267), and hingement of the same stage of left valve (**d**) from sample no. 8 (SUM-CO-1268). **3**. A-1 stage carapace of same specimen in external view (**a**-**c**) from sample no. 20h (SUM-CO-1280), and hingement of the same stage of left valve (**d**) from sample no. 20h (SUM-CO-1281). **4**. A-2 stage carapace of same specimen in external view (**a**-**c**) from sample no. 20h (SUM-CO-1282), and hingement of the same stage of left valve (**d**) from sample no.20h (SUM-CO-1283). **5**. A-1 stage carapace of same specimen in external view (**a**-**c**) from sample no. 23 (SUM-CO-1290), and hingement of the same stage of left valve (**d**) from sample no. 23 (SUM-CO-1291). **6**. A-2 stage carapace of same specimen in external view (**a**-**c**) from sample no. 23 (SUM-CO-1292), and hingement of the same stage of left valve (**d**) from sample no. 23 (SUM-CO-1293). **7**. A-1 stage carapace of same specimen in external view (**a**-**c**) from sample no. 19 (SUM-CO-1301), and hingement of the same stage of left valve (**d**) from sample no. 19 (SUM-CO-1302). **8**. A-2 stage carapace of same specimen in external view (**a**-**c**) from sample no. 19 (SUM-CO-1303), and hingement of the same stage of left valve (**d**) from sample no. 19 (SUM-CO-1304). Scale bars = 100 μm. (A for a-c; B for d)

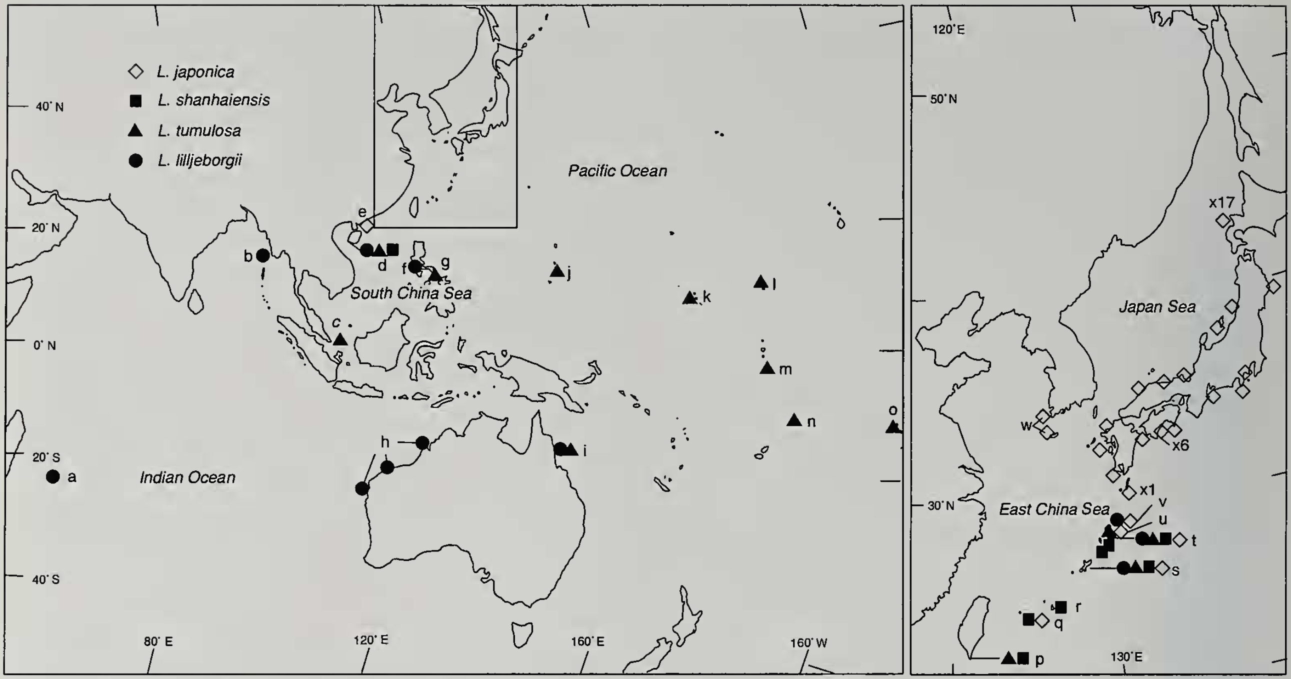

Figure 12. Geographic distributions of four species of *Loxoconcha japonica* species group (Recent). **a** (Mauritius; Brady, 1868); **b** (Burma; Gramann, 1975); **c** (Sunda Shelf; Mostafawi, 1992); **d** (Hainan Island; Gou, 1990); **e** (Hong Kong); **f** (Manila Bay; Keij, 1954); **g** (Cebu Island); **h** (West Australian Coast; Hartmann and Hartmann, 1978); **i** (Lizard Island; Behrens, 1991); **j** (Guam); **k** (Truk); **l** (Marshall Islands); **m** (Gilbert Islands); **n** (Samoa); **o** (Tuamotu Islands; Hartmann, 1984); **p** (South Taiwan); **q** (Sekisei-sho); **r** (Miyako Island); **s** (Okinawa); **t** (Yoron Island); **u** (Tokuno-shima Island); **v** (Amami-o-shima Island); **w** (southern part of Korean Peninsula; Choe, 1984MS); **x** 1–17 (Japan coast; x6 = Uranouchi Bay; Ishizaki, 1968). e, g, and **j-n** (R. Ross, pers. comm., 2002).

from the Middle Pleistocene Shimo-jiro Formation from the Okino-erabu Island of the Ryukyus (Loc. I: Figure 2, loc. h). This species also occurs in two Late Pleistocene formations from Taiwan, the Hengchun Limestone (Locs. D and E: Figure 2, locs. 11 and 12) and the Tungshiao Formation (Loc. F: Figure 2, loc. k).

Recent distribution (Figure 12).—*L. lilljeborgii* is widely distributed over lower latitude coastal regions of the Indian Ocean (Locs. a and b), the South China Sea (Locs. d and f), the northern part of Australia (Locs. h and i) and the Ryukyus (Locs. s, t and v: Figure 2, locs. 17, 19 and 20). *L. tumulosa* is distributed over lower latitudes in the West Pacific coastal regions of the South China Sea (Locs. c, d and g), the northeastern part of Australia (Loc. i), many islands of the West Pacific (Locs. j–o), Taiwan (Loc. p: Figure 2, loc. 23), and the Ryukyus (Locs. s–u: Figure 2, locs. 18–20). *L. japonica* is distributed over lower-to middle latitude coastal regions from Hong Kong to Japan (Locs. e, q, s, t, u, v, w and x1–17: Figure 2, locs. 1–20 and 22). *L. shanhaiensis* is only distributed over the lower latitude coastal regions of Hainan Island (Loc. d), Taiwan (Loc. p: Figure 2, loc. 23) and the Ryukyus (Locs. q–t: Figure 2, locs. 17 and 19–22).

The dispersal and evolution of the four species can be inferred from these data (Figure 13). Firstly, *L. lilljeborgii* and *L. tumulosa* were distributed over the Indian Ocean in the Late Miocene. Secondly, these species migrated from the Indian Ocean to the West Pacific Ocean during the Early Pliocene. Based on morphological and ontogenetic information, together with biogeographic data, *L. japonica* evolved from the northern population of *L. tumulosa.* Finally, *L. shanhaiensis* evolved from the southern population of *L. japonica* in the Middle Pleistocene. These inferences are discussed in greater detail below.

Discussion

Paleobiogeographic and ontogenetic changes in the carapace morphology of the *L. japonica* species group from East Asia are the key to interpreting the phylogeny of the group. In the preceding section, we deduced that *L. japonica* evolved from *L. tumulosa* in the Early Pliocene. In *L. japonica*, the lateral outline and the surface ornamentation change in the A–1 instar and the A–2 instar, respectively. In contrast, in *L. tumulosa*, the lateral outline and the surface ornamentation change in the adult and the A–1 instar, respectively. Futhermore, in *L. japonica*, the alate ridge, which is a common character among the juvenile stages of

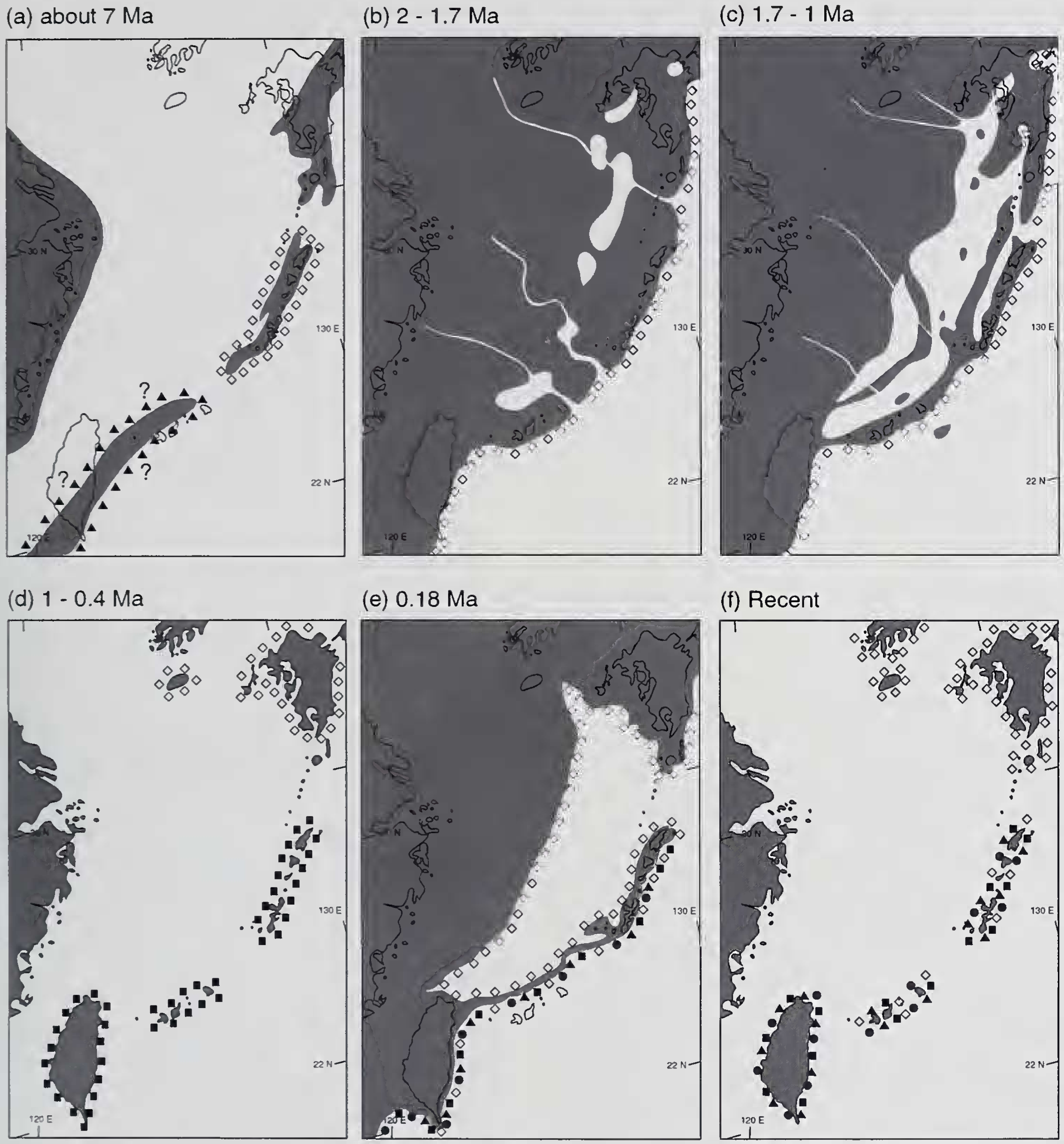

Figure 13. Paleobiogeographic distribution of *Loxoconcha japonica* species group around the Ryukyus. Shaded zones are land areas. *Loxoconcha japonica* Ishizaki, 1968 (open diamond shapes), *Loxoconcha shanhaiensis* Hu, 1981 (solid squares), *L. tumulosa* (Hu, 1979) (solid triangles) and *L. lilljeborgii* (solid circles). Paleogeographic reconstructions are after (a), Ujiié (1986); (b)–(d), Kimura (1996); (e), Ujiié and Nakamura (1996).

all four species, disappears in most adult specimens. From this evidence, the carapace characters of *L. japonica* are considered to have developed by peramorphosis. Moreover, it was deduced that *L. shanhaiensis* differentiated from *L. japonica* in the Middle Pleistocene. In *L. shanhaiensis*, ontogenetic changes of the lateral outline and the surface ornamentation are delayed by one stage, and the adult stage retains the alate ridge. These data indicate that the carapace characters of *L. shanhaiensis* are derived from *L. japonica* by paedomorphosis.

A heterochronic process results from the modification of the relationships among three parameters-age, size and shape-which are assumed to be independent (Gould, 1977). Peramorphosis and paedomorphosis are each subdivided into three processes, and heterochronic evolution is described by one or more of these six processes (Kluge, 1988). In many taxa, it is generally assumed that age is equivalent to size when dealing with fossils, but in fact the relationship between age and size is not always correlative. In the case of ostracods, each instar can be compared in relative age, but relative age does not always correspond to absolute age. If it is assumed that the relative age equals the absolute age, we can consider age and size to be independent of each other. We cannot decide which of the six processes can be applied to the heterochronic evolution of the *L. japonica* species group, because we lack information on the earliest ontogenetic stage of each species. Nonetheless, we can state that either peramorphosis or paedomorphosis has occurred. If the number of moltings is the same among the four species, then it is likely that *L. japonica* became differentiated from *L. tumulosa* by predisplacement and *L. shanhaiensis* was derived from *L. japonica* by post-displacement. To solve these phylogenetic problems, it is essential to clarify the life history of the species in culturing experiments (Ikeya and Kato, 2000).

Table 2. Measurements of valve of *Loxoconcha japonica* Ishizaki, 1969 from sample nos. 1, 6, 8 and 17. Abbreviations: Av = average; OR = observation range; N = number of specimens; M = male; F = female; R = right; L = left.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		*N*
			Av.	OR	Av.	OR	
Suttu Bay (1)	M	R	0.65	0.63–0.67	0.45	0.43–0.46	15
	M	L	0.66	0.64–0.69	0.44	0.41–0.46	14
	F	R	0.58	0.55–0.62	0.42	0.40–0.45	27
	F	L	0.59	0.55–0.64	0.43	0.40–0.45	29
Kagoshima (6)	F	L	0.54	0.49–0.60	0.40	0.38–0.44	24
Misaki (8)	M	R	0.59	0.56–0.64	0.40	0.38–0.43	30
	M	L	0.60	0.57–0.64	0.40	0.37–0.44	36
	F	R	0.54	0.51–0.61	0.39	0.36–0.43	42
	F	L	0.55	0.52–0.61	0.40	0.37–0.44	46
Amami Is. (17)	M	R	0.59	0.55–0.64	0.40	0.37–0.43	30
	M	L	0.59	0.56–0.64	0.41	0.37–0.43	29
	F	R	0.54	0.49–0.58	0.38	0.35–0.41	58
	F	L	0.54	0.50–0.59	0.39	0.35–0.43	64

Systematic descriptions

Order Podocopida G. W. Müller, 1894
Suborder Podocopina Sars, 1866
Superfamily Cytheracea Baird, 1850
Family Loxoconchidae Sars, 1925
Subfamily Loxoconchinae Sars, 1925
Genus ***Loxoconcha*** Sars, 1866

Loxoconcha japonica Ishizaki, 1968

Figures 3.1–3.3, 3.6; 5A, 5a; 7A; 9.1, 9.2

Loxoconcha japonica Ishizaki, 1968, p. 28, 29, pl. 2, fig. 1, pl. 6, figs. 10–12; Ishizaki, 1971, p. 86, pl. 3, fig. 21; Okubo, 1980, p. 416–418, figs. 12, 13, 18a–d; Hu, 1981, p. 77, pl. 3, fig. 7; Kamiya, 1988a, pl. 1, figs. 1–7, text-figs. 4, 5, 7, 8, 10, 11, 13; Kamiya, 1988b, pl. 1, figs. 1–6; Kamiya, 1988c, pl. 1, figs. 9–16; Kamiya, 1989a, pl. 1, figs. 1–8, 13, 14, 17, pl. 2, figs. 1–3, 10, text-figs. 1–8; Kamiya, 1989b, figs. 3, 4, 6, 7, 9, 11, 12; Ruan and Hao, 1988, p. 323, pl. 57, figs. 11–13; Lee, 1990, p. 358, pl. 34, figs. 3, 4; Ikeya and Suzuki, 1992, pl. 5, fig. 9; Kamiya and Hazel, 1992, figs. 1, 3, 4, pl. 1; Kamiya and Nakagawa, 1993, pl. 5, figs. 11, 12; Ozawa, 1996, pl. 6, fig. 5; Cao, 1998, pl. 3, figs. 16–19; Irizuki *et al.*, 1998, fig. 3-5; Yamane, 1998, pl. 6, fig. 2; Yasuhara and Irizuki, 2001, pl. 6, fig. 12.

Loxoconcha impressa (Baird). Kajiyama, 1913, p. 9, pl. 1, figs. 50, 51.

Loxoconcha sp. Hanai, 1961, p. 371, text-fig. 12, figs. 4a, b; Igo and Ikeya, 1971, p. 204, fig. 13.

Loxoconcha sp. A. Ishizaki, 1968, p. 34, pl. 7, figs. 4, 5; Ishizaki, 1971, p. 88, pl. 3, fig. 16.

? *Loxoconcha japonica* Ishizaki. Hu, 1979, p. 69–70, pl. 2, figs. 32–37, text-fig. 8; Hu, 1984, pl. 4, figs. 24–26; Cai, 1982, pl. 3, fig. 21.

Non *Loxoconcha japonica* Ishizaki. Hu, 1981, pl. 3, figs. 1–4, 8, text-fig. 14; Hu, 1983, pl. 2, figs. 3, 4, 6; Hu, 1986, pl. 4, figs. 22, 28, 30, 31; Nohara and Ohshiro, 1992, fig. 6.

Types.—Holotype, a male left valve, IGPS coll. cat. no. 90260; paratypes, a male right valve, IGPS coll. cat. no. 90261, a female left valve, IGPS coll. cat. no. 90262.

Type locality.—St. 303 (33°24.6′N. 133°26.5′E), Uranouchi Bay, Kochi Prefecture, Shikoku, Japan, Recent, coarse sand, depth 25 m (×6 in Figure 12).

Diagnosis.—Large sexual dimorphism; in lateral view, male more elongate and highest more posteriorly than the other three species described here from the *L. japonica* group. Carapace subrhomboidal in lateral view. Dorsal margin straight and sloped toward anterior in male, arched dorsally in female; anterior margin with an oblique infracurvature; ventral margin concave at mid-anterior portion; posterior margin broadly rounded at posteroventral portion. No prominent caudal process. In dorsal view, carapace diamond-shaped, often wedge-shaped in some females. In posterior view, carapace generally elliptical, often egg-shaped in female. Ornamentation consists of concentrically arranged reticulation. Boot-shaped male copulatory organ has trapezoidal basal capsule, triangular distal lobe and basally inflated L-shaped ductus ejaculatorius.

Dimensions.—Length and height of adult males and fe-

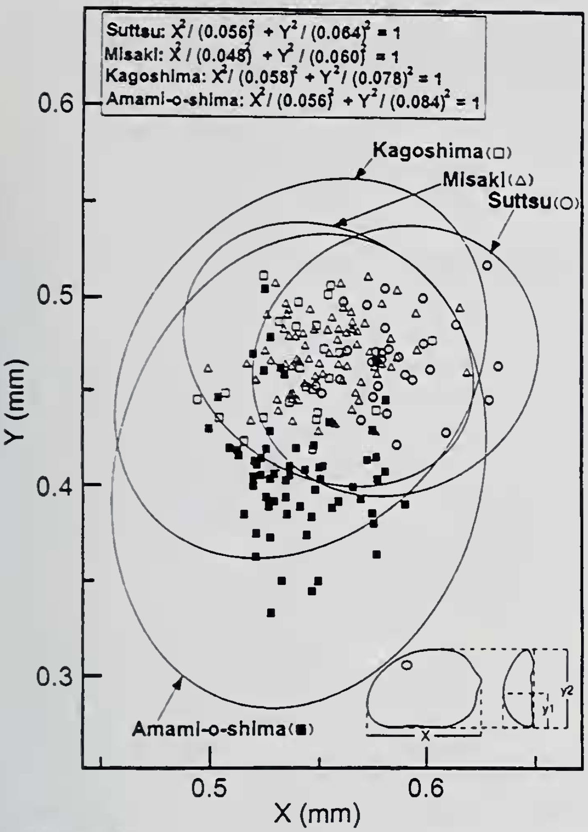

Figure 14. Geographic variation in posterior view of females of *Loxoconcha japonica* Ishizaki, 1968. Symbols refer to Suttsu population (open circles; n = 29), Misaki population (open triangles; n = 76), Kagoshima population (open squares; n = 24) and Amami-o-shima population (solid squares; n = 63). Plot of the distance from the base of ventral margin to the point on the marginal line of the maximum width (y1)/height (y2) on the posterior view of left valve (Y = y1/y2) versus length in the lateral view (X), with series of rejection ellipses with 95% confidence intervals.

males from the sample nos. 1, 6, 8 and 17 are listed in Table 2.

Occurrences.—Fossil (Figure 11): Early Pliocene Maja Formation from Kume Island; Pliocene Sawane Formation from Sado Island; Late Pliocene Yonabaru Formation from Okinawa Island; Pleistocene formations and Holocene deposits and boring core samples from Honshu to Cheju Island, southern Taiwan and Hong Kong. Recent (Figure 12): Japan (Hokkaido-Iriomote Island), southern coast of Korean Peninsula and Hong Kong.

Remarks.—Some specimens from Recent material from the Ryukyus and fossils from the Ryukyus to Taiwan, have an alate ridge on the posteroventral area (see Ruan and Hao, 1988, pl. 57, fig. 13). The alate ridge is especially developed in southern female specimens with an egg-shaped outline in posterior view (Figure 14); this ridge is not developed in males. *L. impressa* reported by Kajiyama (1913) belongs to this species, based on carapace outline, surface ornamentation and the shape of the male copulatory organ. In the illustration of the male copulatory organ by Okubo (1980) it appears that the distal part of the ductus ejaculatorius extends beyond from the illustrated figure. However, we think that his specimen has been crushed and modified in shape.

Loxoconcha shanhaiensis Hu, 1981

Figures 4.1, 4.2, 4.5; 5B, 5b; 6; 7B; 9.3, 9.4

Loxoconcha shanhaiensis Hu, 1981, p. 76, 77, pl. 3, figs. 5, 9, 11, text-figs. 13a, b; Hu, 1982, p. 180, 182, pl. 2, fig. 23; Hu, 1984, pl. 4, figs. 21–23, 27.

Loxoconcha japonica Ishizaki. Hu, 1981, pl. 3, figs. 1–4, 8, text-fig. 14; Hu, 1983, pl. 2, figs. 3, 4, 6; Hu, 1986, pl. 4, figs. 22, 28, 30, 31; Nohara and Ohshiro, 1992, fig. 6.

Types.—Holotype, TNUM. 4148; paratypes, TNUM. 4151, 4153 and 4150.

Type locality.—The west margin of the Hengchun Table land, near Shanhai-li, 80–90 m above sea level, about 3 km west of Hengchun City, southern Taiwan (E in Figure 11).

Diagnosis.—In lateral view, carapace subtrapezoidal and ornamented by concentric coarse reticulations. Boot-shaped male copulatory organ has trapezoidal basal capsule, subtriangular distal lobe, a shoehorn-shaped ductus ejaculatorius and a triangular clasping apparatus.

Description.—**Carapace**: Strong sexual dimorphism. Carapace subtrapezoidal, highest at posterior cardinal angle in lateral view. Dorsal margin straight and sloped toward anterior; anterior margin with an oblique curvature and well developed denticulations; ventral margin straight; posterior margin with broad flat zone, broadly rounded in posteroventral area, with several strong spines. Short but prominent caudal process. In dorsal view, carapace wedge-shaped with maximum width about one-third of length from posterior end. Ornamentation consists of concentrically arranged coarse reticulation. Prominent alate ridge developed in posteroventral area extended toward posterior. **Pore system**: (a) Lateral (sieve-type) pore system. 67 pores distributed on each valve in adult specimens. (b) Marginal pore system includes 16 pores (Figure 5b). **Hinge** (Figure 4.5a, b): Gongylodont. Hinge-line nearly straight. In left valve, anterior element is a downturned claw, median element has 39–42 teeth, and posterior element is a ball-like knob. The hinge of the right valve is complementary. **Muscle scars** (Figure 4.5a, b): Row of 4 adductor muscle scars curved anteriorly at inside of median to slightly anterior of ventromedian of carapace. The upper of the two middle ones elliptical with hollows at middle, the other three scars bean-shaped. Elliptical frontal scar inclines anteroventrally in front of middle two scars. Two divided mandibular scars in front of lowest adductor muscle scars. Fulcral point absent. **Marginal infoldment** (Figure 5b): Widest in anteroventral region, twisted in middle of ventral region and narrowed posterodorsally. **Appendages**: Antennule (Figure 6A). Five segments (there are six segments, but 4th and 5th are fused). Length ratio between distal segments is 26:19:8:29:19. Costae well developed in 2nd, 3rd and 4th segments. Second segment has numerous short hairs on the anterior margin and a short seta on the posterior margin. Third segment has a short seta on the anterior distal end. Fourth segment has two short and three long setae. Fifth segment with four long setae on the distal end. **Antenna** (Figure 6B): Four articulated segments (there are five segments actually, but the 3rd and 4th are fused). Length ratio between distal segments is 26:11:46:4. Costae well developed, especially broad in the anterior margin of 3rd segment. Second segment has a long two-segmented exopodite and a seta on the posterior margin. Third segment has a pair of unequal long setae and numerous hairs on the anterior margin one-sixth of the distance from the proximal end. Along the posterior margin of the 3rd segment, three unequal-sized long setae and numerous hairs are developed in the middle of the ledge and one-third of the distance from the distal end. Furthermore, the third segment bears a seta on the posterior distal end. Fourth segment has two very well developed terminal claws with numerous serrations. **Mandible** (Figure 6C): Five-segmented. Length ratio between two propodite segments and three endopodite segments is 25+: 16:8:12:5. Basal segment (coxa) with eight teeth and a seta on anterior distal margin. Second segment of protopodite (basis) bears an exopodite reduced to a seta. First and 2nd segments of endopodite almost fused. First segment of endopodite with two long setae on the ventral distal end. Second segment of endopodite with a pair of setae on the proximal and ventral distal ends, respectively. Furthermore, the 2nd segment has two setae on the anterior dorsal margin and a seta on the anterior distal margin. Third segment of endopodite with three pairs of setae on the distal end. **Maxilla** (Figure 6D): Extremely thin branchial plate (exopodite) with 16 setae. Basal segment bears a palp and three masticatory processes. Palp indistinctly two-segmented. The proximal segment bears 4 setae on its anterior distal end. Distal segment with three setae on the distal end and one seta on the ledge in the posterior proximal end. Outer, middle and inner masticatory processes bear 5, 4 and 5 setae, respectively, on each distal end. **Thoracic legs** (Figure 6E, F and G): All three legs are 4-segmented, similar in shape. Length ratio between distal segments is 24:20:8:13 in 3rd thoracic leg. Costae developed on both margins. First segment having a seta on the anterior proximal end and two setae on the anterior proximal end. The segment has a seta on the posterior proximal end. Second segment bearing numerous hairs along the anterior margin and a seta on the anterior distal end. Third and 4th segments bearing numerous hairs along the anterior margin. **Copulatory organ** (Figure 7B): The basal capsule, with costae in the margin, is trapezoidal. A large subtriangular distal lobe and a small clasping apparatus are developed on the distal end of the basal capsule. Small shoehorn-shaped ductus ejaculatorius.

Table 3. Measurements of valve of *Loxoconcha shanhaiensis* Hu, 1981 from sample nos. 17 and 20. Abbreviations same as Table 2.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		*N*
			Av.	OR	Av.	OR	
Amami Is. (17)	M	R	0.48	0.45–0.51	0.33	0.31–0.37	29
	M	L	0.49	0.46–0.54	0.33	0.31–0.36	27
	F	R	0.48	0.46–0.52	0.34	0.32–0.36	26
	F	L	0.48	0.44–0.53	0.34	0.31–0.37	42
Okinawa Is. (20)	M	L	0.50	0.44–0.52	0.33	0.32–0.34	12
	F	L	0.49	0.46–0.53	0.34	0.32–0.38	40

Dimensions.—Length and height of adult males and females from the sample nos. 17 and 20 are given in Table 3.

Occurrences.—Fossil (Figure 11): Middle Pleistocene Shimo-jiro Formation from Okino-erabu Island; Late Pleistocene Tungshiao Formation and Hengchun Limestone from Taiwan. Recent (Figure 12): Ryukyus (Amami Island to Iriomote Island), Taiwan and Hainan Island.

Remarks.—Specimens reported by Hu (1981, 1983, 1986) and Nohara and Ohshiro (1992) as *L. japonica* have coarse reticulation, straight dorsal margin sloped toward the anterior, posterior margin with broad flat zone and several strongly developed spines, so these specimens are identified as *L. shanhaiensis*.

Loxoconcha tumulosa (Hu, 1979)

Figures 4.3, 4.4, 4.6; 5C, 5c; 9.5, 9.6

Loxocorniculum tumulosum Hu, 1979, p. 71, 72, pl. 2, figs. 17, 21, 22, 26, 27, 30, 31, text-fig. 10.

Loxoconcha tumulosa (Hu). Hu, 1981, p. 78, pl. 3, figs. 6, 7; Hu, 1984, pl. 4, figs. 17, 18, 20; Zhao *et al.*, 1985, pl. 20, fig. 11; Gou, 1990, p. 25, pl. 3, figs. 45–47.

Loxoconcha alata Brady. Guha, 1968, p. 61, pl. 4, figs. 5, 13.

Loxoconcha heronislandensis Hartmann. Hartmann, 1984, p. 128, pl. 7, figs. 1–6, text-figs. 47, 48; Whatley and Zhao, 1987, p. 350, pl. 5, fig. 12; Behrens, 1991, pl. 5, figs. 5, 6.

Loxoconcha sp. Hartmann and Hartmann, 1978, pl. 10, fig. 6.

Non *Loxoconcha tumulosa* (Hu). Zhao and Wang, 1988, pl. 2, fig. 27.

Types.—Holotype, TUM. 4033; paratypes, TUM. 4034–4036, 4065, 4066.

Type locality.—A road cut from Hengchun to Oluanpi, 15–20 m above sea level, about 1 km east of Nanwan,

Table 4. Measurements of valve of *Loxoconcha tumulosa* (Hu. 1979) from sample no. 23. Abbreviations same as Table 2.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		*N*
			Av.	OR	Av.	OR	
Taiwan (23)	F	R	0.51	0.50–0.53	0.33	0.33–0.34	10
	F	L	0.52	0.50–0.54	0.35	0.34–0.36	7

Table 5. Measurements of valve of *Loxoconcha lilljeborgii* Brady, 1868 from sample no. 17. Abbreviations same as Table 2.

Sample (No.)	Sex	Valve	Length (mm)		Height (mm)		*N*
			Av.	OR	Av.	OR	
Amami Is. (17)	M	R	0.51	0.47–0.54	0.34	0.32–0.36	78
	M	L	0.52	0.49–0.55	0.34	0.32–0.36	69
	F	R	0.50	0.46–0.54	0.34	0.32–0.39	95
	F	L	0.50	0.45–0.54	0.35	0.31–0.37	97

Pingtung Prefecture, southern Taiwan (D in Figure 11).

Diagnosis.—Large sexual dimorphism; in lateral view, male more elongate. Carapace rhomboidal in lateral view. Dorsal and ventral margins nearly parallel; anterior margin with an oblique infracurvature, and developed denticulations; posterior margin broadly rounded in posteroventral area. Prominent caudal process. In dorsal view, carapace wedge-shaped. In posterior view, carapace egg-shaped. Ornamentation consists of very coarse oncentrically arranged reticulation. Prominent alate ridge developed at postero-ventral area, and protuberance developed in posterodorsal area.

Dimensions.—Length and height of adult males and females from the locality sample no. 23 is listed in Table 4.

Occurrences.—Fossil (Figure 11): Late Miocene Round Chalk and Silt Formation, Pliocene Guiter Formation from the Andaman Islands of the Indian Ocean and Late Pleistocene Hengchun Limestone from Taiwan. Recent (Figure 12): Ryukyus (Tokuno-shima to Okinawa), Taiwan, Hainan, Cebu Island, Lizard Island, Guam, Truk, Marshall Islands, Gilbert Islands, Samoa and Tuamotu Islands from Southwest Pacific.

Remarks.—Specimens reported by Guha (1968) from the Late Miocene and the Pliocene sediments of Interview Island and Guiter Island as *L. alata* are identified as *L. tumulosa*. *L. heronislandensis* reported by Behrens (1991) also belongs to this species. A specimen reported by Zhao and Wang (1988) as *L. tumulosa* differs from this species, because it has a protruded anterior margin and does not have a posterodorsal protuberance.

Loxoconcha lilljeborgii Brady, 1868

Figures 3.4, 3.5, 3.7; 5D, 5d; 7C; 9.7, 9.8

Loxoconcha lilljeborgii Brady, 1868, p. 183, pl. 13, figs. 11–15; Mostafawi, 1992, p. 151, pl. 5, fig. 102.

Loxoconcha lilljeborgii Brady? Whatley and Zhao, 1987, p. 351, pl. 5, fig. 13.

Loxoconcha lilljeborchi Brady. Keij, 1954, p. 358, pl. 3, fig. 4; Guha, 1968, p. 61, pl. 4, fig. 20; Gramann, 1975, pl. 5, figs. 6–8; Zhao *et al.*, 1985, pl. 20, fig. 12; Zhao and Wang, 1988, pl. 2, fig. 26.

Loxoconcha georgei Hartmann and Hartmann, 1978, p. 105, pl. 9, figs. 15, 16, text-figs. 259–268, (non) pl. 9, figs. 13, 14; Howe and Mckenzie, 1989, p. 24, figs. 8, 84, 85, 154; Behrens, 1991, p. 116, 117, pl. 4, figs. 6–9.

Loxoconcha broomensis Hartmann and Hartmann, 1978, p. 106, pl. 10, fig. 1, text-figs. 272, 279, (non) pl. 10, figs. 2–4, text-figs. 269, 280.

Loxocorniculum sp. 1, Tabuki *et al.*, 1987, pl. 2, fig. 11; Tabuki and Nohara, 1990, pl. 2, fig. 11; Tabuki, 1992, pl. 1, fig. 15.

Loxocorniculum sp. A. Tabuki and Nohara, 1988, pl. 1, figs. 13, 14.

Loxocorniculum cf. (*Loxoconcha*) *georgei* Hartmann. Tabuki and Nohara, 1995, fig. 4–8.

Loxocorniculum georgei (Hartmann). Gou, 1990, p. 26, pl. 3, figs. 43, 44.

Types.—Not defined.

Type locality.—Mauritius, Indian Ocean (a in Figure 12).

Diagnosis.—Strong sexual dimorphism; in lateral view, male more elongate. Carapace subrhomboidal in lateral view. Dorsal margin nearly straight in male, arched dorsally in female; anterior margin with an oblique infracurvature; ventral margin concaved in mid-anterior area; posterior margin broadly rounded in posteroventral area. Caudal process not prominent. In dorsal view, carapace elongate arrowhead-shaped. In posterior view, egg-shaped. Ornamentation consists of concentrically arranged oblong pits. Prominent protuberance developed in posterodorsal area. Pear-shaped male copulatory organ has inflated trapezoidal basal capsule, subtriangular distal lobe, a leaf-shaped clasping apparatus and elongate ductus ejaculatorius.

Dimensions.—Length and height of adult males and females from the sample No. 17 is given in Table 5.

Occurrences.—Fossil (Figure 11): Late Miocene Round Chalk and Silt Formation, Pliocene Guiter Formation from the Andaman Islands of the Indian Ocean, and Late Pleistocene Hengchun Limestone from Taiwan. Recent (Figure 12): Ryukyus (Tokuno-shima to Okinawa), Taiwan, Hainan, and Lizard Island from Southwest Pacific.

Remarks. — Specimens reported from the Ryukyus as *Loxocorniculum* sp. 1 (by Tabuki *et al.*, 1987; Tabuki and Nohara, 1990; Tabuki, 1992), *Loxocorniculum* sp. A (by Tabuki and Nohara, 1988) and *Loxocorniculum* cf. (*Loxoconcha*) *georgei* (Tabuki and Nohara, 1995) are identified as *L. lilljeborgii*, with its carapace outline, concentrically arranged oblong pits and postero-dorsal alate ridge. Hartmann and Hartmann (1978) described *Loxoconcha georgei* as a new species, and figured carapaces of both sexes and male soft parts, but a type specimen was not designated. Judging from the carapace ornamentation, we think the figured male and female specimens belong to different species. The male specimens we identify as *L. lilljeborgii*, with its concentrically arranged oblong pits, nearly straight dorsal margin, developed posterodorsal alate ridge and identically shaped of male copulatory organ. On the other hand, the female specimens are *Loxoconcha broomensis*, which was described in the same paper. This specimen has two strong anterior ridges. Carapaces of both sexes and the male soft parts of *L. broomensis* were also figured by Hartmann and Hartmann (1978), but a type specimen was not designated. Judging from the carapace outline and ornamentation, the female specimen should be identified as *L. lilljeborgii.*

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